BIOMETRIC STUDY OF *BARREMITES SUBDIFFICILIS* (KARAKASCH)

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ABSTRACT. A study is made of allometric growth in four dimensions of the ammonite *Barremites subdifficilis* (Karakasch) from the Neocomian of the Crimea. The four dimensions are further analysed simultaneously by the multivariate statistical method of principal component analysis. The results are compared with those found for two species of Triassic ammonites.

IT is often assumed by quantitative paleontologists that there will be an allometric growth relationship between many of the dimensions of the coiled ammonite shell. Obata (1959) investigated several species of Desmoceratidae and found almost isometric growth for most combinations of the variables studied but in a certain number of cases possibly significant positive and negative allometric growth.

In the present analysis the variables studied are maximum diameter of shell (x_1), maximum diameter of umbilicus (x_2), height of last whorl (x_3), breadth of last whorl (x_4); all measurements are in millimetres. The measurements were converted to base 10 logarithm values for the bivariate and quadrivariate studies.

The material was collected by Dr. V. V. Drushshits, Department of Paleontology, University of Moscow, who also checked the measurements. The specimens are stored in the University of Moscow; all (32) specimens were derived from the same bed in the Barremian sequence of the Crimea, U.S.S.R. The quadrivariate computations were performed on the computers of the Swedish Board for Computing Machinery, who provided free machine time. Part of the study was supported by a grant from the Swedish Natural Science Research Council. This study was completed during the junior author's tenure of a fellowship from the Southern Fellowships Fund, Chapel Hill, North Carolina, U.S.A.

RELATIVE GROWTH ANALYSIS

Standard least squares regression was used in the allometric analyses. The equations between pairs of variables are:

$$x_1 = 7{\cdot}04x_2^{0{\cdot}76} \qquad (1)$$
$$x_1 = 2{\cdot}43x_3^{0{\cdot}93} \qquad (2)$$
$$x_1 = 2{\cdot}99x_4^{0{\cdot}99} \qquad (3)$$
$$x_2 = 0{\cdot}39x_3^{1{\cdot}04} \qquad (4)$$
$$x_2 = 0{\cdot}45x_4^{1{\cdot}14} \qquad (5)$$
$$x_3 = 1{\cdot}43x_4^{0{\cdot}99} \qquad (6)$$

The exponents of equations (2), (3), (4), and (6) differ so slightly from unity that there can be little doubt that growth in these cases is isometric. Equations (1) and (5) are indicative of possible allometric growth. The 95 per cent. confidence intervals for the regression coefficients of these two equations were computed. For equation (1) it was found that $0{\cdot}69 < \beta < 0{\cdot}84$, where β is the population regression coefficient. Thus there

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is only a 5 per cent. chance of the population coefficient lying outside of these limits; hence it may be concluded that growth here is of the negative allometric kind. For equation (5) the 5 per cent. confidence intervals for the regression coefficient are $1{\cdot}07 < \beta < 2{\cdot}00$. The lower limit does not include unity and it may be suggested that a slight positive allometric relationship exists between x_2 and x_4.

PRINCIPAL COMPONENT ANALYSIS

The covariance matrix for the logarithmically transformed observations of the four variables is ($N = 32$)

$$\mathbf{S} = (32-1)^{-1}\begin{pmatrix} 0{\cdot}5942 & 0{\cdot}6753 & 0{\cdot}5975 & 0{\cdot}5547 \\ 0{\cdot}6753 & 0{\cdot}8831 & 0{\cdot}6631 & 0{\cdot}6393 \\ 0{\cdot}8831 & 0{\cdot}6631 & 0{\cdot}6405 & 0{\cdot}5573 \\ 0{\cdot}5547 & 0{\cdot}6393 & 0{\cdot}5573 & 0{\cdot}5626 \end{pmatrix}.$$

The eigenvalues and eigenvectors of this matrix were extracted with the aid of an electronic computer. They are given in the following table.

Eigenvalues	*Percentage of total variation*	*Eigenvectors*
$\lambda_1 = 0{\cdot}08166$	94·44	$\mathbf{b}'_1 = (0{\cdot}480, 0{\cdot}570, 0{\cdot}486, 0{\cdot}458)$
$\lambda_2 = 0{\cdot}00314$	3·63	$\mathbf{b}'_2 = (0{\cdot}194, -0{\cdot}790, 0{\cdot}547, 0{\cdot}200)$
$\lambda_3 = 0{\cdot}00131$	1·50	$\mathbf{b}'_3 = (-0{\cdot}065, -0{\cdot}169, -0{\cdot}522, 0{\cdot}833)$
$\lambda_4 = 0{\cdot}00037$	0·37	$\mathbf{b}'_4 = (0{\cdot}853, -0{\cdot}153, -0{\cdot}438, -0{\cdot}239)$

The first principal component accounts for almost all of the variation. Together with the second component, 98 per cent. of the total variation may be explained. It is interesting to observe that all variables are roughly equally balanced in the first principal component, which implies that the four dimensions participate equally in the variability of the shell morphology. The second principal component is mainly concerned with variation in log x_2 and log x_3; that is there is a shape relationship between umbilical diameter and height of whorl. The third principal component is representative of variation in height and width of whorl; it could be shown to be statistically significant by Lawley's test (1956).

To the extent of the writers' knowledge, this is the first time a principal component analysis has been made on the test of an ammonite and there is therefore no comparative literature available. In order to gain some impression of the importance of the above figures, two principal component analyses were run on Triassic ammonites, the data being taken from Kummel and Steele (1962). The observations were transformed logarithmically as before.

(*a*) *Dieneroceras spathi* Kummel and Steele (Kummel and Steele 1962, p. 659). The material ($N = 42$) derives from Elko County, Nevada, and Cottonwood Canyon, California (zone of *Meekoceras gracilitatum*).

The covariance matrix is:

$$\mathbf{S} = (42-1)^{-1}\begin{pmatrix} 0{\cdot}5419 & 0{\cdot}5831 & 0{\cdot}3770 & 0{\cdot}4764 \\ 0{\cdot}5831 & 0{\cdot}7772 & 0{\cdot}4007 & 0{\cdot}4747 \\ 0{\cdot}3770 & 0{\cdot}4007 & 0{\cdot}3058 & 0{\cdot}3490 \\ 0{\cdot}4764 & 0{\cdot}4747 & 0{\cdot}3490 & 0{\cdot}4738 \end{pmatrix}.$$

The eigenvalues and eigenvectors of this matrix are presented in the following table.

Eigenvalues	*Percentage of total variation*	*Eigenvectors*
$\lambda_1 = 0{\cdot}046445$	90·73	$\mathbf{b}'_1 = (0{\cdot}526, 0{\cdot}603, 0{\cdot}377, 0{\cdot}467)$
$\lambda_2 = 0{\cdot}003614$	7·06	$\mathbf{b}'_2 = (0{\cdot}153, -0{\cdot}754, 0{\cdot}282, 0{\cdot}573)$
$\lambda_3 = 0{\cdot}000729$	1·42	$\mathbf{b}'_3 = (-0{\cdot}241, -0{\cdot}027, 0{\cdot}881, -0{\cdot}405)$
$\lambda_4 = 0{\cdot}000399$	0·78	$\mathbf{b}'_4 = (0{\cdot}801, -0{\cdot}260, -0{\cdot}036, -0{\cdot}538)$

(*b*) *Meekoceras gracilitatum* White (Kummel and Steele 1962, p. 694); the material is from Elko County, Nevada, U.S.A. (Zone of *M. gracilitatum*); it comes from several beds. The covariance matrix is ($N = 43$):

$$\mathbf{S} = (43-1)^{-1}\begin{pmatrix} 1{\cdot}1672 & 1{\cdot}5413 & 0{\cdot}9800 & 1{\cdot}0675 \\ 1{\cdot}5413 & 2{\cdot}2879 & 1{\cdot}3173 & 1{\cdot}3681 \\ 0{\cdot}9800 & 1{\cdot}3173 & 0{\cdot}8604 & 0{\cdot}9112 \\ 1{\cdot}0675 & 1{\cdot}3681 & 0{\cdot}9112 & 1{\cdot}0649 \end{pmatrix}.$$

The eigenvalues and eigenvectors of this matrix are given below.

Eigenvalues	*Percentage of total variation*	*Eigenvectors*
$\lambda_1 = 0{\cdot}121998$	95·23	$\mathbf{b}'_1 = (0{\cdot}471, 0{\cdot}653, 0{\cdot}403, 0{\cdot}434)$
$\lambda_2 = 0{\cdot}004907$	3·74	$\mathbf{b}'_2 = (0{\cdot}221, -0{\cdot}706, 0{\cdot}187, 0{\cdot}647)$
$\lambda_3 = 0{\cdot}000799$	0·62	$\mathbf{b}'_3 = (0{\cdot}475, -0{\cdot}273, 0{\cdot}559, -0{\cdot}623)$
$\lambda_4 = 0{\cdot}000517$	0·40	$\mathbf{b}'_4 = (-0{\cdot}709, 0{\cdot}031, 0{\cdot}700, 0{\cdot}074)$

It will be observed that in both cases the first principal component accounts for more than 90 per cent. of the total variation. Moreover, the contributions of each of the dimensions are approximately equal; this was also found to be so for *Barremites subdifficilis*. In fact, if one computes the angle between the theoretical vector $\mathbf{k}' = (0{\cdot}5, 0{\cdot}5, 0{\cdot}5, 0{\cdot}5)$ and each of the first eigenvectors for the three species here discussed, it is found that it is in all cases roughly zero degrees, which implies accordance with the hypothesis of equal contribution by all dimensions.

The second principal component is for the Cretaceous ammonite mainly indicative of covariation in variables log x_2 and log x_3, while for the two Triassic ammonites log x_2 and log x_4 covary. For all three species the third principal component represents covariation in variables log x_3 and log x_2.

These results are enlightening. They disclose the perhaps surprising situation that diameter of shell, umbilical diameter, height of whorl, and breadth of whorl are possibly equally important in the morphologic variation of ammonites. The remaining principal components tend to differ with respect to the sign and magnitude of the components of the eigenvectors connected with them. It is conceivable that these components may be of specific significance and that the vector of principal components could be of taxonomic use in characterizing a species. In the following table we supply the mean vector for the principal components of each species (computed from the equation $\bar{\mathbf{y}} = \mathbf{B}'\bar{\mathbf{z}}$, where $\mathbf{B}$ is the matrix of eigenvectors and $(\mathbf{z}_1, ..., \mathbf{z}_4) = (\log \mathbf{x}_1, ..., \log \mathbf{x}_4)$).

Species	*Mean vector of principal components*
Barremites subdifficilis	$\bar{\mathbf{y}}_1 = (1{\cdot}974, -0{\cdot}316, 0{\cdot}075, 0{\cdot}351)$
Meekoceras gracilitatum	$\bar{\mathbf{y}}_2 = (2{\cdot}433, 0{\cdot}920, 0{\cdot}314, -0{\cdot}310)$
Dieneroceras spathi	$\bar{\mathbf{y}}_3 = (2{\cdot}127, 0{\cdot}317, -0{\cdot}056, 0{\cdot}323)$

CONCLUSIONS

The growth relationships between the variables maximum diameter of shell, umbilical width, height of last whorl, and breadth of last whorl are for *Barremites subdifficilis* (Karakasch) almost isometric. Slight negative allometric growth could be shown to exist between maximum diameter and umbilical diameter and slight positive allometric growth was shown to occur between umbilical diameter and breadth of the last whorl.

The covariance matrix of these variables was subjected to the multivariate statistical method of principal component analysis, whereby the total variation is broken up into components of variation. In order to provide our conclusions with a somewhat more general basis two species of Triassic ammonites were also analysed by the same method. The results show that almost all of the biologic variation in the shells of these ammonites with respect to the variables studied is contained in the covariation of these variables studied and that each of these contributes equally to the variation. This result would appear to vindicate the common use of these four dimensions in the description of ammonites. It would seem possible that the mean vector of principal components might be useful in the characterization of species.

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